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Stuck amongst introduced species: Trophic ecology reveals complex relationships between the critically endangered Niau kingfisher and introduced predators, competitors and prey

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Abstract

The introduction of mammals on oceanic islands currently threatens or has caused the extinction of many endemic species. Cats and rats represent the major threat for 40 % of currently endangered island bird species. Direct (predation) and/or indirect (exploitative competition for food resource) trophic interactions are key mechanisms by which invaders cause the decrease or extinction of native populations. Here, we investigated both direct and indirect trophic interactions amongst four predator species (i.e. animals that hunt, kill and feed on other animals), including three introduced mammals (*Felis silvestris catus*, *Rattus rattus* and

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Rattus exulans) and one critically endangered native bird, the Niau kingfisher (*Todiramphus gertrudae*). All four species' diets and prey availability were assessed from sampling at the six main kingfisher habitats on Niau Island during the breeding season. Diet analyses were conducted on 578 cat scats, 295 rat digestive tracts (218 *R. exulans* and 77 *R. rattus*) and 186 kingfisher pellets. Despite simultaneous use of morphological and PCR-based methods, no bird remains in cat and rat diet samples could be assigned to the Niau kingfisher, weakening the hypothesis of current intense predation pressure. However, we determined that Niau kingfishers mainly feed on introduced and/or cryptogenic prey and highlighted the potential for exploitative competition between this bird and both introduced rat species (for Dictyoptera, Coleoptera and Scincidae). We recommend removing the cats and both rat species, at least within kingfisher breeding and foraging areas (e.g. mechanical or chemical control, cat sterilisation, biosecurity reinforcement), to simultaneously decrease predation risk, increase key prey availability and boost kingfisher population dynamics.

Keywords
Island bird conservation, Introduced mammals, Predation, Competition, *Todiramphus gertrudae*, *Felis silvestris catus*, *Rattus* spp.

Introduction

Islands, which host almost 40% of the critically endangered species on Earth on less than 6% of its total land area, are particularly vulnerable to biological invasions and represent a global conservation priority (Tershy et al. 2015). The long history of anthropogenic transportation of alien species to islands worldwide, including those of East Polynesia (e.g. since 1200–1300 A.D. in Wilmshurst et al. 2011), has resulted in deleterious effects on native wildlife that has often evolved without defences against predators or competitors (Steadman 2006; Anderson 2009). Alien (i.e. introduced) species inevitably disturb the natural balance of island food webs by modifying trophic links. This may affect the demography and abundance of native (and introduced) species, with further cascading effects (Courchamp et al. 2003; White et al. 2006; David et al. 2017).

Interactions like predation and competition shape the structure and dynamics of food webs in communities (Chase et al. 2002) and are critical considerations in species conservation and management (e.g. Brown et al. 2014; Marshall et al. 2016). Direct predation (i.e. top-down effect) is the predominant mechanism by which invaders can dramatically decrease populations of native species or even cause their extinction (Doherty et al. 2016; David et al. 2017). Introduced cats and rats have been identified as a prime cause of more than half the extinctions of island bird species recorded over the last centuries and still represent the major threat to 40% of currently endangered island bird species (Doherty et al. 2016; McCreless et al. 2016). Exploitative competition is an indirect mechanism of introduced species impact, leading to numerous native population declines but less often to extinctions (Davis 2003; David et al. 2017). Usually, local species restrict their realised niche and/or shift their niche to sub-optimal habitats to reduce niche overlap with introduced species (Reitz and Trumble 2002; Rankin et al. 2018).

Better understanding the feeding ecology of a threatened endemic species through diet analysis is an essential step towards its long-term conservation and management

(e.g. Gooch et al. 2015; Resano-Mayor et al. 2016). Trophic analyses also reveal complex trophic interactions between sympatric introduced and native species, particularly relevant to islands simultaneously threatened by several introduced species. For example, predation rates can be estimated (e.g. Bonnaud et al. 2009) and the potential for exploitative competition or competitive exclusion evaluated by measuring trophic overlaps between species (e.g. Du Preez et al. 2017). However, when prey are numerous and not limiting, high diet overlap does not necessarily imply significant competition (Cupples et al. 2011). Diet studies evaluating the environmental availability of shared resources are also required, to better assess the consequences of trophic interactions (White et al. 2006).

Here, we focused on one of the most threatened bird species worldwide, the Critically Endangered (BirdLife International 2016) Niau kingfisher *Todiramphus gertrudae*, whose sole population is confined to the small and remote atoll of Niau (Tuamotu Archipelago, French Polynesia). This human-modified and inhabited island hosts a range of cryptogenic and introduced species, including three of the most significant invasive predators worldwide: the pacific rat *Rattus exulans*, the black rat *Rattus rattus* and the feral cat *Felis silvestris catus*. *Rattus exulans* was probably introduced from South East Asia during the Polynesian colonisation of the archipelago ca. AD 1200 (Wilmshurst et al. 2011), while *R. rattus* and *F. s. catus* were likely introduced with the late 18th century arrival of European settlers (Atkinson 1985; Duffy and Capece 2012). Recently, a demographic study (Kesler et al. 2012) suggested that Niau kingfisher population dynamics could be limited by strong predation by cats and rats at critical demographic stages. Competition for food resources with introduced predators has also been suspected of impacting bird survival (Gouni and Sanford 2003; Coulombe et al. 2011). However, insufficient data is available from which to construct a robust conservation strategy.

This study aimed to identify possible trophic interactions (namely, predation and exploitative competition) between three introduced mammals and the Niau kingfisher during its reproductive season. We analysed the diet of these four 'sympatric' species for shared or exclusive prey to (i) identify the principal prey in the Niau kingfisher diet, (ii) quantify direct predation by introduced predators on kingfishers and (iii) evaluate trophic overlaps and identify prey taxa potentially at risk from exploitative competition, based on estimated prey availability. Such detailed understanding of the multi-invaded island food web should provide useful input to future restoration and conservation strategies.

Materials and methods

Study site

Niau Atoll (16°9'15"S, 146°21'20.4"W) (Tuamotu Archipelago, French Polynesia, South Pacific Ocean) (Figure 1), probably colonised by humans over 1000 years ago and regularly visited since 1820 (Butaud 2007), has a current resident population of ca. 200. Niau Island measures 26 km² and culminates at 6 m above sea level (Andréfouët et al. 2005). Its climate is tropical and oceanic (Mueller-Dombois and Forsberg 1998).

The vegetation consists of three main formations: (i) feo forest, a dense forest growing on jagged fossilised limestone coral covering 1800 ha of the atoll, (ii) *Cocos nucifera* plantations covering 700 ha, of which only 10% is used for copra farming and (iii) wetlands dominated by shoreline purslane *Sesuvium portulacastrum* and Jamaica swamp sawgrass *Cladium mariscus* (Butaud 2007).

The Niau kingfisher *T. gertrudae*

This endemic bird is confined to Niau and preferentially nests and forages within coconut groves located on the east side of the island, especially in semi-open and exploited groves (Gouni et al. 2006; Coulombe et al. 2011; Thibault and Cibois 2017) (Figure 1). Between 1970 and 1990, the Niau kingfisher was reported as common (Seitre and Seitre 1992), with a population estimated at 400–600 individuals (Holyoak and Thibault 1984). The reasons for its decline in the early 2000s remain unknown, but hypotheses include introduced mammalian predators (Kesler et al. 2012) and/or land-use changes (decreased coconut harvesting and use of fire to clear coconut plantations) (Coulombe et al. 2011; Thibault and Cibois 2017). Currently, the population has stabilised at ~140 individuals (100 mature individuals) (Thibault and Cibois 2017). To breed, the Niau kingfisher excavates the trunks of dead coconut trees, where it nests, tending to return to territories and partners over several years (Gouni and Sanford 2003; Holyoak and Thibault 1984). The breeding season lasts from October to February and both parents undertake parental duties until juveniles are independent (Kesler et al. 2012). To date, the few field observations available on the kingfisher's diet suggest that it mainly forages on terrestrial arthropods (Araneidea, Coleoptera, Dermaptera, Anisoptera) and lizards (Scincidae and Gekkonidae) (Holyoak and Thibault 1984; Marie 2006).

Predator diet analysis

Sample types and collection

Sampling was conducted at two periods yearly over two consecutive years (from November 2009 to March 2011): the first in November at the beginning of kingfisher reproduction (laying, incubating and hatching periods) and the second in February-March at the end of the breeding season (fledgling and feeding periods of juveniles). Predators' diet samples and prey availability were sampled from six habitat types within surveyed kingfisher territories: two feo forests (low < 8 m and high > 8 m), three coconut plantations (abandoned, cultivated and intensively cultivated) and a wetland (Figure 1).

Rats were trapped in each habitat along a 320 m transect of 40 equally-spaced Victor (model BM201, Forest Stewardship Council, USA) snap-traps, set over five consecutive nights, baited with coconut flesh before dusk and checked early in the morning. Trapped rats were identified at the species level, weighed, sexed and dissected. Their

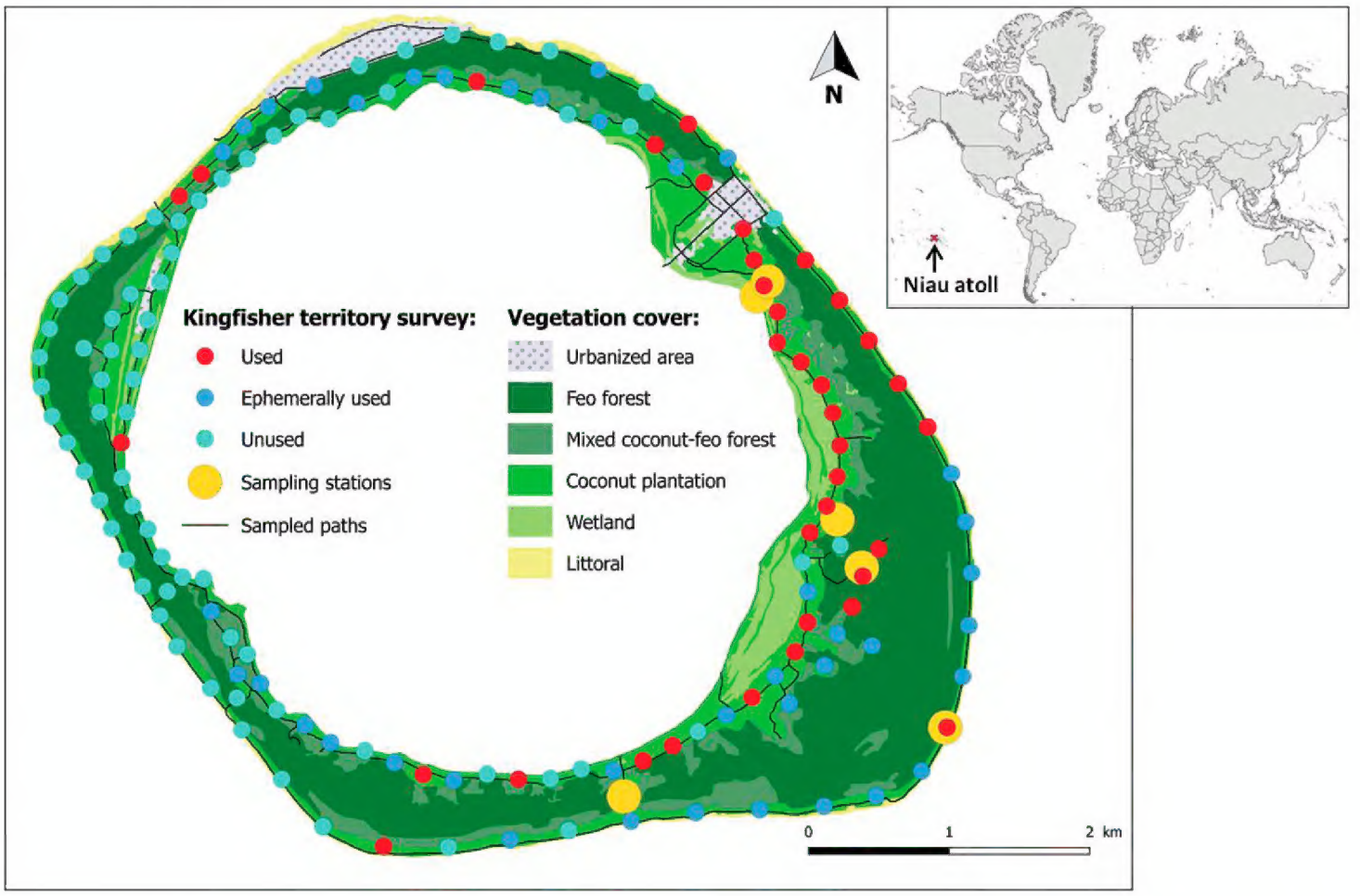


Figure 1. Map of Niau Atoll (Tuamotu Archipelago, French Polynesia). Location of the six sampling stations (rat diet samples and prey availability) and sampled paths (cat diet samples), surveyed Niau kingfisher territories (Coulombe et al. 2011) and main habitat types (Butaud 2007).

guts were collected and stored in 90% ethanol during transport and then frozen until examination. Cat scats were collected across all island paths, stored in Ziploc bags (SC Johnson, USA) and frozen until analysis. Kingfisher pellets were collected during the final field session (March 2011; end of reproductive season) below nests or hunting perches. The entire set of analysed diet samples consisted of 186 kingfisher pellets, 578 cat scats and 295 rat digestive tracts (218 *R. exulans* and 77 *R. rattus*).

To evaluate the availability of the main potential prey groups, the density of 16 different taxa (i.e. rats, Scincidae, Amphipoda, Isopoda and twelve terrestrial arthropod Orders) was estimated within the six studied habitats in February and November 2010 (see Suppl. material 1 for a detailed description of sampling protocols).

Diet analysis

Morphological diet analyses were conducted on all the collected diet samples. Each rat's stomach contents and three last non-expelled faeces were individually extracted, homogenised and the entire volume analysed. Kingfisher pellets were dried before analysis and cat scats were analysed by washing over a 0.5 mm sieve under a stream of hot water. All hard prey remains (e.g. hairs, feathers, bones, scales, chitin) were isolated and identified to the finest taxonomic level possible under a dissecting microscope by comparison with reference materials from field-collected specimens and

via identification keys (for details, see Zarzoso-Lacoste et al. 2013, 2016). When possible, lizards were identified at the family level (Gekkonidae, Scincidae), arthropods at the order level (for Coleoptera, Hymenoptera, Orthoptera, Hemiptera, Dictyoptera, Dermaptera, Lepidoptera, Diptera, Odonata, Scorpiones, Araneae, Decapoda, Amphipoda and Isopoda) and Myriapoda at the subphylum level (containing Diplopoda and Chilopoda classes). Gastropoda and fish (Teleostei) were identified at the class and infra-class level, respectively. Birds were identified at the finest taxonomic level possible and assigned to the Aves class level in further statistical analyses. Mammalian prey corresponded only to the *Rattus* genus. Plants were only reported as presence/absence data for both omnivorous rat species.

To maximise the detection and identification of Niau kingfisher DNA in cat and rat diet samples, we implemented a PCR-based method (see Zarzoso-Lacoste et al. 2013, 2016) targeting the 5' end of the multi-copy mitochondrial cytochrome c oxidase subunit I gene (Cox1), a standard barcode sequence that enables species-level discrimination in birds (Hebert et al. 2004). This molecular method includes the combined use of three bird-specific primer pairs that were selected for their high power of detection, their specificity and their sensitivity towards bird DNA in cat and rat diet samples (for details, see: Zarzoso-Lacoste et al. 2016). This protocol notably deals with cases where bird soft tissue (e.g. vitellus, embryo or flesh) were consumed: our protocol is able to detect and identify bird DNA (including the DNA of the Niau kingfisher) at concentrations as low as 0.01 ng.μl^{-1} (the lowest concentration tested in vitro using dilution series; see Zarzoso-Lacoste et al. 2016). Furthermore, we previously demonstrated that the molecular protocol systematically performs better in both the detection and the resolution of the taxonomic identification of birds in the diet samples of their predators than the morphological method (including samples where no hard remains of prey were found; see Zarzoso-Lacoste et al. 2016).

Data analyses

All analyses were performed using the Statistical Software R version 3.5.1 (R Development Core Team 2018) – see Suppl. material 2 for the original data used to perform the following analyses.

Diet descriptors

To describe each predator's overall diet and for each of the above prey taxa, several indices were calculated from (i) number of Prey Occurrences (*PO*) and (ii) Minimum Number of Individuals (*MNI*; White 1953). Prey Occurrence Frequency (*POF* = *PO/S*) indicates the frequency of a prey category in predator diet samples, "*S*" being the total number of samples per predator. Mean Prey Number (*MPN* = *MNI/S*) indicates the mean abundance of a prey category in predator diet samples. To more accurately evaluate the intensity of predator consumption on a particular prey category "i", we

assessed (i) $P_{iPN} = MNI_i/\sum MNI$, the proportion of this prey relative to the total number of animal prey ingested by each predator and (ii) $MPN_i = \sum(MNI_i/PO_i)$ reflecting the predation pressure on this prey. Finally, we constructed a bipartite network to visualise links between predators and their shared or exclusive prey, using *MNI* data and the *bipartite* R package (Dormann et al. 2008).

Diet comparison based on identified animal prey

We performed all subsequent analyses using *MNI* data for the 21 identified animal prey taxa (excluding plants and unidentifiable lizards and terrestrial arthropods). Abundance-based diet data were square-rooted prior to analysis to reduce the influence of the most abundant taxa (Clarke and Warwick 2001).

Sampling representativeness, diet richness and diversity

We used sample-size-based Hill numbers (orders q = 0, 1 and 2), plus interpolated and extrapolated accumulation curves to estimate (i) the sampling representativeness of each predator diet and prey availability based on taxonomic richness (q = 0) and (ii) predator diet diversity using the exponential Shannon's entropy index (giving more weight to rare species, q = 1) and the inverse of Simpson's concentration index (giving more weight to abundant species, q = 2) (Chao et al. 2014). We then compared their diet diversity up to the same base sample size (here, m = 1473 prey *MNI*, see Chao et al. 2014 for more information), using the package iNEXT (Hsieh et al. 2016). Corresponding 95% confidence intervals were obtained by a bootstrap method based on 999 replications.

Identification of indicator prey in predators' diet

To identify the prey or combination of prey either included in the diet of a particular predator and/or contributing most to niche overlaps, we conducted "indicator species analyses" using the *multipatt* and *strassoc* functions of the *indicspecies* package (De Caceres and Legendre 2009). We used the *signassoc* function with 999 permutations and Sidak's correction for multiple comparisons to compare the abundance of prey taxa in predator diets.

Prey selection

We computed the Jacobs' electivity index (D; Jacobs 1974) to investigate whether these four predators consumed prey proportionately to their relative densities in the environment. This index ranges between -1 (negative selection) and +1 (positive selection), indicating whether a prey species is selected, respectively, less or more than proportionate to its availability. We performed chi-square tests with Bonferroni adjustment to test for the significance of prey selection by the studied predators.

Diet dissimilarity, breadth and overlap

We measured interspecific niche separation and intraspecific variability amongst predator diet samples using a Bray-Curtis dissimilarity matrix. We calculated the mean dissimilarity *(MD)* of diet composition between and within predator species using the *meandist* function of the *vegan* package (Oksanen et al. 2018). We then compared predator diets using a permutation-based test with the *betadisper* and *permutest* functions, corrected with Tukey's 'Honest Significant Difference' method for multiple comparisons. To visualise patterns in dietary dissimilarity within and amongst species in a low dimensional space, we performed Nonmetric Multidimensional Scaling (*NMDS*) using the *metaMDS* function. Finally, we calculated predator Diet Breadth (*DB*; from 0-specialised diet-to 1-generalist diet-) and Diet Overlap (*DO*; from 0 -no overlap- to 1 -complete overlap -), using the *nichevar* and *nicheoverlap* functions of the *indicspecies* package. Corresponding 95% confidence intervals were obtained by a bootstrap method based on 999 replications.

Results

Diet composition of studied predators

Kingfishers almost exclusively prey on terrestrial arthropods (*PiPN* = 50%; see Suppl. material 3), lizards (40%) and Decapoda (9%) (Figure 2[1]). The terrestrial arthropod taxa Coleoptera (23%), Hymenoptera (10%, of which 92% were Formicidae) and Dictyoptera (9%) were the most frequently and abundantly preyed upon. Scincidae were the most consumed lizards (23%) but Gekkonidae were also widely eaten (11%). Of these prey, Scincidae, Gekkonidae, Decapoda, Araneae and Coleoptera were strongly and significantly associated with the kingfisher diet (*component A* > 0.63) (Tables 1, 2).

The cat diet mainly consisted of rats (49%), followed by terrestrial arthropods (28%) and lizards (10%) (Figure 2[1], see Suppl. material 3). Dictyoptera were the terrestrial arthropods most frequently and abundantly consumed (8%), followed by Dermaptera (5%) and Coleoptera (2%). Gekkonidae were the most consumed lizards (4%). Rats and fish were significantly associated with cat diet samples (Tables 1, 2).

The rat diet was mainly plants (mainly coconut flesh, *POF* = 89% and 94% for *R. exulans* and *R. rattus*, respectively), but included a large proportion of animal prey (Figure 2[1], see Suppl. material 3). Terrestrial arthropods were the animal prey consumed most by both *R. exulans* and *R. rattus* (*PiPN* = 82% and 75%, respectively), followed by lizards (11% and 7%, respectively). *R. rattus* preyed more frequently on lizards, Gastropoda and crustacean than *R. exulans*. For both rats, Scincidae were the most consumed lizards (6% and 3% for *R. exulans* and *R. rattus*, respectively). Of the identified terrestrial arthropods, *R. exulans* and *R. rattus* mainly consumed Dictyoptera (11% and 8%, respectively), Hymenoptera (25% and 20%, respectively, all Formicidae), Diptera (11% and 8%, respectively, mainly larvae) and Coleoptera (7% and 4%, respectively). Hemiptera, Isopoda and Amphipoda were indicator prey particularly present in the *R. rattus* diet (Tables 1, 2).

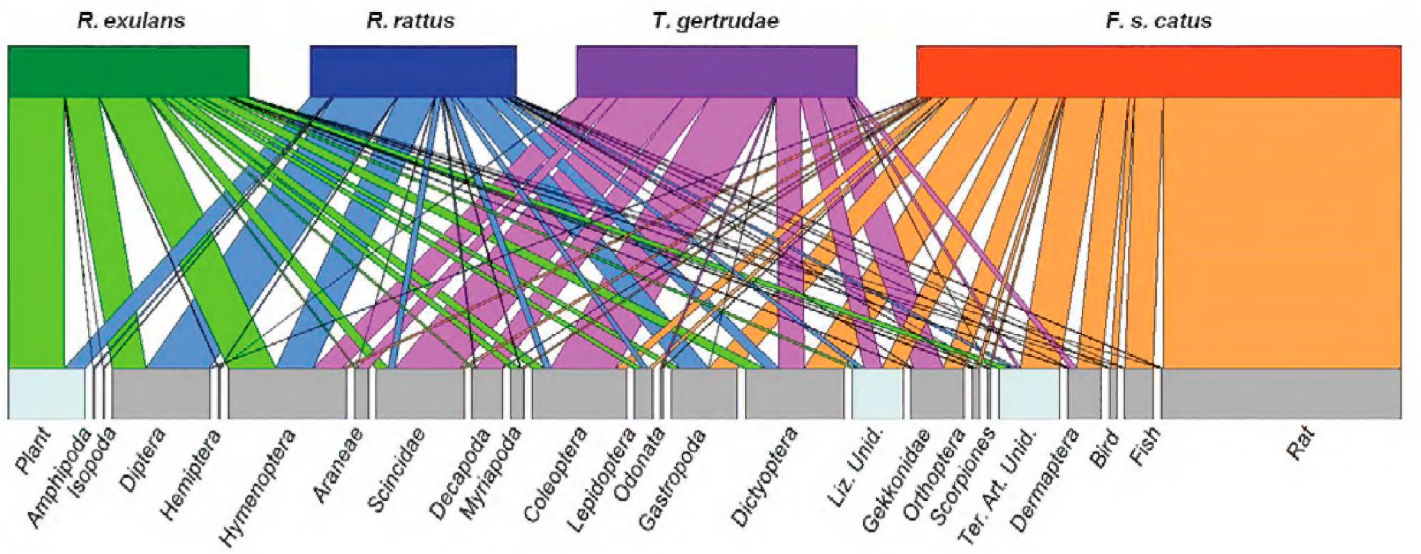
Table 1. Prey as indicators of predators' diet. Patterns and strength of the association between prey taxa and predators' diet. *Component A*: probability that the surveyed predator belongs to the target predator group given the fact that the prey taxon has been found in the diet. *Component B*: probability of finding the prey taxon in diet samples belonging to the predator group.

	Prey	*Component A*	*Component B*	*p* value
T. gertrudae	Scincidae	0.69	0.80	< 0.001
	Gekkonidae	0.74	0.44	< 0.001
	Coleoptera	0.63	0.76	< 0.001
	Decapoda	0.82	0.44	< 0.001
	Araneae	0.81	0.17	< 0.001
	Odonata	0.88	0.02	0.05
	Scincidae + Coleoptera	0.88	0.61	< 0.001
F. s. catus	Rat	0.95	0.97	< 0.001
	Fish	0.87	0.17	< 0.001
R. rattus	Hemiptera	0.73	0.07	< 0.001
	Isopoda	0.87	0.03	0.01
	Amphipoda	0.73	0.03	0.03
T. gertrudae + *R. rattus*	Scincidae	0.84	0.66	< 0.001
	Coleoptera	0.82	0.63	< 0.001
R. rattus + *R. exulans*	Diptera	0.99	0.24	< 0.001
	Myriapoda	0.93	0.08	< 0.001
	Lepidoptera	0.89	0.06	0.01
	Orthoptera	0.85	0.06	0.01
R. rattus + *F. s. catus*	Gastropoda	0.87	0.14	< 0.001
T. gertrudae + *R. exulans* + *R. rattus*	Dictyoptera	0.86	0.40	< 0.001
	Hymenoptera	0.98	0.33	< 0.001

Table 2. Prey as indicators of predators' diet. Test and comparison of the association between prey taxon and each predator diet. Values in bold highlight the predator that more significantly (< $p_{adjusted}$-Sidak-) consumed a particular prey than random.

	T. gertrudae	*F. s. catus*	*R. exulans*	*R. rattus*	$p_{adjusted}$
Gekkonidae	**< 0.001**	1.00	1.00	1.00	0.004
Scincidae	**< 0.001**	1.00	1.00	0.89	0.004
Coleoptera	**< 0.001**	1.00	1.00	0.80	0.004
Araneae	**< 0.001**	1.00	0.96	0.93	0.004
Decapoda	**< 0.001**	1.00	1.00	0.97	0.004
Odonata	**0.01**	0.81	1.00	1.00	0.047
Rat	1.00	**< 0.001**	1.00	1.00	0.004
Fish	1.00	**< 0.001**	1.00	0.99	0.004
Bird	1.00	**< 0.001**	0.77	0.57	0.008
Dermaptera	0.04	**< 0.001**	0.99	0.95	0.004
Myriapoda	1.00	1.00	**0.01**	0.12	0.036
Hymenoptera	0.84	1.00	0.23	**< 0.001**	0.004
Dictyoptera	0.35	1.00	0.82	**< 0.001**	0.004
Gastropoda	1.00	0.33	0.99	**< 0.001**	0.004
Orthoptera	1.00	0.96	0.26	**0.01**	0.047
Diptera	1.00	1.00	0.07	**0.01**	0.028
Hemiptera	0.84	1.00	0.69	**0.01**	0.020
Isopoda	1.00	1.00	0.46	**0.01**	0.032
Lepidoptera	1.00	0.98	0.18	**0.03**	0.129
Amphipoda	1.00	1.00	0.43	**0.06**	0.219
Scorpiones	0.76	0.50	0.46	**0.31**	0.771

1)



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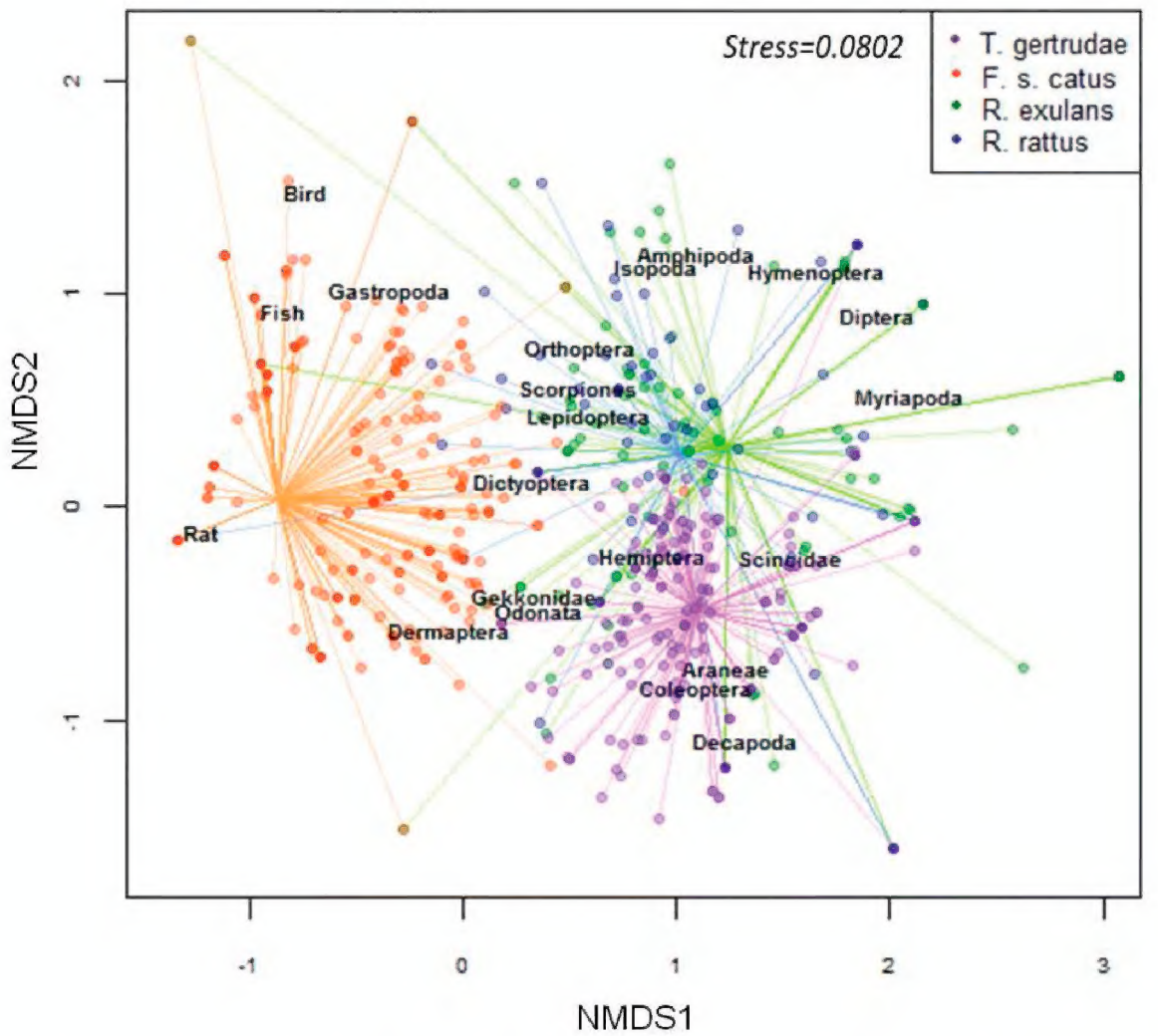

Figure 2. Diet composition and overlap within and amongst the four studied predators. **1** Bipartite network. Lower boxes correspond to the identified (dark grey) and unidentified (light grey) prey taxa consumed by predators. Line and prey box widths show how frequently prey taxa are consumed by predators. Liz. Unid.: lizard unidentified, Terr. Art. Unid.: terrestrial arthropod unidentified. **2** *nMDS* of abundance-based Bray-Curtis dissimilarity of predator diet samples (solid dots). Solid lines represent the dispersion of a particular sample compared to the barycentre of its predator group.

Morphological and PCR-based methods, used in combination, allowed the detection of 28 bird individuals in cat (n = 20) and rat (n = 3 and 5 for *R. rattus* and *R. exulans*, respectively) diet samples and the identification of 24 of them as belonging to the

following seven species; *Gygis alba*, *Ptilinopus coralensis*, *Anous stolidus*, *Gallus gallus*, *Sterna bergii*, *Puffinus lherminieri* and *Accrocephalus atyphus* (for details, see Zarzoso-Lacoste et al. 2016). None was assigned to the Niau kingfisher.

Sampling representativeness, diet richness and diversity

Rarefied and extrapolated species-accumulation curves (See Suppl. material 4) tended to saturate, indicating accurate sampling of predators' diet and mean prey availability in the environment. Diversity accumulation curves revealed that kingfishers presented the lowest prey richness (q_0D = 12.9), although their prey abundance was more equally distributed amongst categories (q_1D = 6.9 and q_2D = 5.8) (See Suppl. material 4). Conversely, cats exhibited intermediate-level prey richness (q_0D = 17), consuming prey categories more unevenly (q_1D = 5.3 and q_2D = 2.9). The two rat diets presented the highest prey richness (q_0D = 21.9 and 20.1 for *R. rattus* and *R. exulans*, respectively), but differed in distribution of prey abundance (q_1D = 9.2 and q_2D = 6.5 for *R. exulans*, q_1D = 7 and q_2D = 4.7 for *R. rattus*).

Diet dissimilarity and breadth

Mean dissimilarities (Table 3) and intra-species dispersion (Figure 2[2]) were highest in *R. rattus* and *R. exulans* diets (but lower for *R. rattus*), while intermediate values were observed for the Niau kingfisher, with the lowest values for cats. Differences were significant for all pairs of predators (permutation test, $p_{adjusted} < 0.001$-TukeyHDS-), except between *R. exulans* and *R. rattus* ($p_{adjusted} = 0.13$) (Table 4). These results are consistent with calculated predator diet breadths (DB, see Suppl. material 3), the two rat species showing the widest diet breadth (0.43, *CI* = 0.42–0.44), closely followed by the kingfisher (0.42, *CI* = 0.41–0.42), while the cats showed the narrowest (0.35, *CI* = 0.33–0.35).

Prey selection

Jacobs' electivity index (*D*) confirmed that the kingfisher positively selected its main prey (i.e. Scincidae, Coleoptera, Hymenoptera, Dictyoptera and Dermaptera) (Table 5). The kingfisher negatively selected Araneae and strongly avoided almost all the other taxa. Of the main kingfisher prey, Dictyoptera and Dermaptera were strongly and positively selected by both rat species and cats ($D > 0.92$, $p < 0.001$; and $D = 1$, $p < 0.001$, respectively). Scincidae, Coleoptera and Hymenoptera were also positively selected by *R. exulans* ($D > 0.76$, $p < 0.001$) and *R. rattus* ($D > 0.62$, $p < 0.001$), while cats slightly positively selected Coleoptera and tended to shun Hymenoptera (D = 0.48 and -0.26, respectively, $p_{adjusted} < 0.001$).

Table 3. Analysis of inter and intra species diet dissimilarities. Mean distance calculated based on the Bray-Curtis dissimilarity matrix between samples of each predator (diagonal) and between each pair of predators.

	T. gertrudae	*F. s. catus*	*R. exulans*	*R. rattus*
T. gertrudae	0.53			
F. s. catus	0.94	0.43		
R. exulans	0.81	0.95	0.82	
R. rattus	0.76	0.92	0.79	0.76

Table 4. Analysis of inter and intra species diet dissimilarities.Results of the Tukey HDS test for significant difference between species pairwise comparisons.

	Difference	**Lower *CI***	**Upper *CI***	$p_{adjusted}$
T. gertrudae – F. s. catus	0.08	0.04	0.12	< 0.001
T. gertrudae – R. exulans	-0.22	-0.27	-0.17	< 0.001
T. gertrudae – R. rattus	-0.16	-0.23	-0.09	< 0.001
R. exulans – F. s. catus	0.30	0.26	0.34	< 0.001
R. rattus – F. s. catus	0.24	0.18	0.30	< 0.001
R. rattus – R. exulans	-0.06	-0.12	0.01	0.13

Table 5. Prey availability and selectivity. Prey availability corresponds to the estimates of the number of prey individuals per Ha sampled over the six main habitat types of Niau Island. Jacobs electivity index (*D*) is calculated for each predator.

	Prey	***R. exulans***		***R. rattus***		***F. s. catus***		***T. gertrudae***	
	Availability	***MNI***	***D***	***MNI***	***D***	***MNI***	***D***	***MNI***	***D***
Scincidae	164	41	**0.81**	22	**0.67**	15	0.18	228	**0.96**
Coleoptera	219	43	**0.76**	24	**0.61**	39	**0.48**	224	**0.95**
Hymenoptera	483	164	**0.89**	130	**0.86**	18	**-0.26**	100	**0.72**
Orthoptera	339	9	-0.04	6	-0.21	13	-0.25	0	**-1.00**
Diptera	3552	117	0.09	220	**0.53**	5	**-0.96**	0	**-1.00**
Hemiptera	4896	3	**-0.97**	6	**-0.93**	0	**-1.00**	2	**-0.98**
Dictyoptera	113	68	**0.92**	51	**0.90**	139	**0.91**	87	**0.92**
Dermaptera	1	8	0.99	3	0.98	86	**1.00**	21	**1.00**
Lepidoptera	317	30	**0.55**	19	0.39	15	-0.15	0	**-1.00**
Odonata	104	0	**-1.00**	0	**-1.00**	3	-0.38	6	0.20
Scorpiones	1	2	0.97	1	0.95	6	0.98	1	0.93
Aranea	1948	6	**-0.82**	2	**-0.93**	0	**-1.00**	41	**-0.31**
Amphipoda	2725	3	**-0.94**	6	**-0.87**	0	**-1.00**	0	**-1.00**
Isopoda	3693	1	**-0.98**	4	**-0.94**	0	**-1.00**	0	**-1.00**
Myriapoda	4	31	**0.99**	6	0.96	9	0.95	0	**-1.00**
Rat	2	2	0.94	4	0.97	829	**1.00**	0	**-1.00**

Diet overlap

Interspecific niche separation was highest between cats and the three other predators (*MD* = 0.92, 0.94 and 0.95 for *R. rattus*, kingfisher and *R. exulans*, respectively), intermediate between *R. exulans* and both kingfisher and *R. rattus* (0.81 and 0.79, re-

spectively) and lowest between kingfisher and *R. rattus* (0.76) (Table 3, Figure 2[2]). These results are consistent with the calculation of diet overlap between predators. Diet overlap was almost complete between the two rat species (*DO* = 0.98, *CI* = 0.96–0.99), intermediate between kingfishers and rats (0.63 *CI* = 0.56–0.70 and 0.57 *CI* = 0.48–0.69 with *R. exulans* and *R. rattus*, respectively) and low between cats and the three other predators (0.21 *CI* = 0.15–0.27 with both Niau kingfisher and *R. rattus* and 0.17 *CI* = 0.13–0.20 with *R. exulans*). The prey taxa contributing most to diet overlaps between the Niau kingfisher and both rat species were Dictyoptera and Hymenoptera (*components A* > 0.86, *B* > 0.33), while *R. rattus* strongly shared two additional prey with this bird (Scincidae and Coleoptera; *components A* > 0.86, *B* > 0.33) (Table 1). Diptera, Myriapoda, Lepidoptera and Orthoptera were strongly shared by the two rat species (*components A* > 0.85), while *R. rattus* only significantly shared Gastropoda with cats (*components A* > 0.86).

Discussion

This study is the first to jointly analyse the diet of an endemic island bird and three of the most harmful introduced predators. We sought to explore complex trophic interactions between native and introduced species on multi-invaded islands and to assess the impact of introduced predators on survival of the critically endangered Niau kingfisher.

First reliable data on Niau kingfisher feeding ecology

Our study offers the first detailed diet analysis of the Niau kingfisher during its chick-rearing period, adding to the limited existing data. Our findings are crucial for the accurate conservation and management of this critically endangered bird.

First, the Niau kingfisher consumes a narrow range of prey taxa, but in regular abundances (i.e. low diet richness but relatively high diversity). Dissimilarity of diet samples is low, suggesting a relatively homogeneous diet. These results support a narrow diet breadth and specialised diet at a population level that make the kingfisher highly vulnerable to exploitative competition for its few main prey.

Second, Gekkonidae, Scincidae, terrestrial arthropods (principally Coleoptera, Dyctioptera and Araneae) and small Decapoda represent crucial resources for adult, nestling and fledgling kingfishers. In particular, Scincidae, Coleoptera, Hymenoptera and Dictyoptera are positively selected (i.e. consumed more than proportionate to their availability in the environment), suggesting that these scarce prey may be potentially at risk for exploitative competition with introduced predators.

Third, some of the Niau kingfisher's main prey are cryptogenic species, probably introduced from South-East Asia by Polynesians over the last centuries (Fisher 1997; Austin 1999; Ineich et al. 2007; Hamilton et al. 2010): *Emoia cyanura*, *E. impar*, *Lipinia noctua*, *Cryptoblepharus poecilopleurus* (Scincidae), *Lepidodactylus lugubris*,

Gehyra oceanica, *G. insulensis* (Gekkonidae) or more recently (late 1980s) for *Hemidactylus frenatus* (Case et al. 1994; Ineich et al. 2007). The latter species, generally considered as aggressive, has the potential to strongly compete and negatively impact local gecko populations (Case et al. 1994). The Niau kingfisher also widely consumes the cosmopolitan Dyctioptera *Pycnoscelus surinamensis*, *Blatella germanica* and *Periplaneta australasiae*, probably more recently introduced in the Tuamotu, at least partly from South Asia (Cochereau 1966; Parker et al. 1977). It is worth noting that the kingfisher likely shifted its nesting and foraging habits with the development and intensification of copra farming on the island, from patches previously dominated by the native palm tree (*Pritchardia mitiaroana*) to areas widely planted with the cryptogenic coconut tree on which this bird currently depends (Coulombe et al. 2011; Thibault and Cibois 2017). Hence, our study illustrates the positive function (e.g. alternative food or habitat resource) which exotic species can perform for island wildlife, particularly in man-transformed landscapes (e.g. Schlaepfer et al. 2011, 2012). Such complex interactions between native and introduced species, often scientifically neglected, need to be considered in restoration and conservation projects to prevent unexpected cascade effects from alien species removal or control.

Trophic interactions between the Niau kingfisher and the three introduced predators

No support for high predation pressure on Niau kingfisher population

Although our study used two complementary approaches (morphological and PCR-based methods) to analyse a large number of cat and rat diet samples (578 cat scats and 295 rat digestive tracts), collected within kingfisher territories during the critical incubating and rearing periods, no bird remains were formally identified as Niau kingfisher. Our results suggest that, if predation by cats and rats does occur, it is much less frequent than suggested by Kesler et al. (2012).

To explain the decline of the Niau kingfisher, Kesler et al. (2012) hypothesised that the low survival of adult females (ca. 40%) might be due to nocturnal rat predation of nests during incubation. This hypothesis is not consistent, however, with the aggressive and territorial behaviour reported for Niau kingfishers, observed chasing rats from nesting trees (Gouni et al. 2006; pers. obs.). Since eggs are rarely left unattended (parents take turns brooding), unlike nestlings (parents often out foraging; G. Coulombe pers. comm.), the nestling stage could be the most vulnerable to rat predation. However, our results do not support this alternative hypothesis either. Kesler et al. (2012) also suggested that cat predation may be responsible for the high mortality of kingfisher juveniles (approximately 90% each year). Although cats are efficient bird predators (Doherty et al. 2016; McCreless et al. 2016) and the behaviour of juvenile kingfishers increases their predation risks (e.g. perching near the ground, calling loudly; Gouni et al. 2006; Kesler et al. 2012; pers. obs.), the absence of kingfisher remains in cat scats do not support this hypothesis either.

Diet overlaps and potential exploitative competition between native and introduced predators

An extensive overlap in diet and food habits may indicate either a high potential for competition between species or a very abundant resource (Cupples et al. 2011). Evaluating whether the interacting predators select their shared prey more than proportionate to their availability in the habitat (positive selection) is therefore critical to untangle these two hypotheses.

On Niau Island, cats presented the narrowest diet breadth and the lowest variability in intraspecific diet composition, suggesting relatively homogeneous and specialised trophic behaviour (low prey richness with few abundantly preyed taxa) of individuals. Although cats and Niau kingfishers shared positively-selected prey (mainly Gekkonidae, but also Coleoptera, Dyctioptera and Dermaptera), their diets only marginally overlapped (DO = 0.21), making competition or competitive exclusion unlikely.

Conversely, both rat species presented generalist trophic behaviour, with the widest diet breadths and inter-individual variability in diet composition. Our study revealed a substantial niche overlap between the Niau kingfisher and both rat species (DO = 0.63 and DO = 0.57 for *R. exulans* and *R. rattus*, respectively). While Dictyoptera and Hymenoptera constitute the main diet overlap between kingfishers and both rat species, Scincidae and Coleoptera are also highly shared by *R. rattus* and kingfishers. Importantly, of the Niau kingfisher's prey, all but Dermaptera were significantly positively selected by both rat species (and more intensively by *R. exulans*), indicating possible exploitative competition with the kingfisher for these highly nutritive and relatively scarce prey (see Table 5). This exploitative competition may reduce the density and availability of Niau kingfisher critical prey (Towns 2002; Rankin et al. 2018), thereby possibly affecting survival at different life-stages (adults, nestlings and fledglings) and/or breeding success.

Conclusion and conservation perspectives

A better understanding of the complex and multiple trophic relationships between endangered natives (here, the Niau Kingfisher) and different invasive alien species should enhance decision-making on invasive species removal for conservation purposes. It should also help to anticipate potential deleterious cascading effects in trophic webs.

Although we do not question the important role that predation by introduced mammalian predators may have played in the past decline of the Niau kingfisher, our results fail to support the hypothesis of a current intense and continuous direct predation on this species. Conversely, our results reveal a substantial diet overlap between the Niau kingfisher and both rat species, suggesting an indirect impact by exploitative competition on key prey taxa (including cryptogenic and introduced species). Considering the critical size of the sole existing population of Niau kingfishers, it is important to avoid any additional mortality due to key prey rarefaction (or even direct preda-

tion). For these reasons, Niau Island was recently listed amongst islands worldwide where introduced mammal eradications are required to prevent imminent extinction of endemic vertebrates (Holmes et al. 2019).

Since rats represent the main prey of cats on Niau Island, cat eradication risks at least temporarily boosting rat populations, with the ensuing impacts on kingfishers from predation and competition (e.g. Courchamp et al. 2003; but see Bonnaud et al. 2010). Thus, the optimal and most time- and cost-efficient management action would be to simultaneously remove cats and both rat species to avoid a potential pernicious trophic cascade (e.g. Zavaleta et al. 2001). This would simultaneously decrease predation risk and increase key prey availability, likely to boost *T gertrudae* population dynamics (Kesler et al. 2012). If such a triple eradication cannot be programmed due to logistics, sociological and/or financial issues, an alternative emergency interim strategy would be to locally control feral cats and rats (e.g. using live or kill traps, bait stations with toxins, feral cat shooting) within the Niau kingfisher's breeding and foraging areas, possibly combined with sterilisation of domestic cats and rat density control in the village, to slow down the recolonisation process of treated areas. In both cases, special care should be taken to (i) monitor the impact on the Niau ecosystem of increased introduced and cryptogenic prey densities following introduced predator management and (ii) reinforce biosecurity to avoid introduced mammal recolonisation of the island (e.g. from the port and airport). The public awareness campaigns conducted by local NGOs (e.g. SOP Manu) and collaborations with local farmers (nesting tree protection with rat-proof metal rings, promotion of mechanical clearing methods rather than fire) should be pursued, to enhance Niau kingfisher conservation.

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References

Anderson A (2009) The rat and the octopus: Initial human colonization and the prehistoric introduction of domestic animals to remote Oceania. Biological Invasions 11: 1503–1519. https://doi.org/10.1007/s10530-008-9403-2

Andréfouët S, Chauvin C, Spraggins S, Torres-Puzilla D, Kranenbourg C (2005) Atlas des récifs coralliens de Polynésie française. Centre IRD de Nouméa, Nouméa. http://www.documentation.ird.fr/hor/fdi:010045822

Atkinson IAE (1985) The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. In: Moors PJ (Ed.) Conservation of Island Birds. International Council for Bird Preservation, Cambridge, 35–81.

Austin CC (1999) Lizards took express train to Polynesia. Nature 397: 113–114. https://doi.org/10.1038/16365

BirdLife International (2016) *Todiramphus gambieri*. The IUCN Red List of Threatened Species. https://www.iucnredlist.org/species/22683499/129640736 [accessed 20 March 2019]

Bonnaud E, Bourgeois K, Vidal E, Legrand J, Corre M (2009) How can the Yelkouan shearwater survive feral cat predation? A meta-population structure as a solution? Population Ecology 51: 261–270. https://doi.org/10.1007/s10144-008-0134-0

Bonnaud E, Zarzoso-Lacoste D, Bourgeois K, Ruffino L, Legrand J, Vidal E (2010) Top-predator control on islands boosts endemic prey but not mesopredator. Animal Conservation 13: 556–567. https://doi.org/10.1111/j.1469-1795.2010.00376.x

Brown DS, Symondson WOC, Burger R, Cole N, Vencatasamy D, Clare EL, Montaxam A (2014) Dietary competition between the alien Asian Musk Shrew (*Suncus murinus*) and a reintroduced population of Telfair's Skink (*Leiolopisma telfairii*). Molecular Ecology 23: 3695–3705. https://doi.org/10.1111/mec.12445

Butaud J (2007) Etude de la flore vasculaire de l'atoll soulevé de Niau, cartographie de sa végétation, caractérisation de l'habitat du Martin-Chasseur de Niau et priorités de conservation. Société d'Ornithologie de Polynésie 'Manu', Papeete.

Case TJ, Bolger DT, Petren K (1994) Invasions and competitive displacement among house geckos in the tropical pacific. Ecology 75: 464–477. https://doi.org/10.2307/1939550

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM (2014) Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. Ecological Monographs 84: 45–67. https://doi.org/10.1890/13-0133.1

Chase JM, Abrams P, Grover JP, Diehl S, Chesson P, Holt RD, Richards SA, Nisbet RM, Case TJ (2002) The interaction between predation and competition: A review and synthesis. Ecology Letters 5: 302–315. https://doi.org/10.1046/j.1461-0248.2002.00315.x

Clarke KR, Warwick RM (2001) Change in marine communities: An approach to statistical analysis and interpretation (2nd edn). PRIMER–E Ltd, 176 pp.

Cochereau P (1966) Compte rendu d'une mission d'inventaire faunistique aux î1es Gambier et Tuamotu. ORSTOM, Nouméa. http://horizon.documentation.ird.fr/exl-doc/pleins_textes/divers12-04/10929.pdf

Coulombe GL, Kesler DC, Gouni A (2011) Agricultural coconut forest as habitat for the critically endangered Tuamotu Kingfisher (*Todiramphus gambieri gertrudae*). The Auk 128: 283–292. https://doi.org/10.1525/auk.2011.10191

Courchamp F, Chapuis J, Pascal M (2003) Mammal invaders on islands: Impact, control and control impact. Biological Reviews 78: 347–383. https://doi.org/10.1017/S1464793102006061

Cupples JB, Crowther MS, Story G, Letnic M (2011) Dietary overlap and prey selectivity among sympatric carnivores: Could dingoes suppress foxes through competition for prey? Journal of Mammalogy 92: 590–600. https://doi.org/10.1644/10-MAMM-A-164.1

David P, Thébault E, Anneville O, Duyck PF, Chapuis E, Loeuille N (2017) Impacts of invasive species on food webs: A review of empirical data. In: Bohan DA, Dumbrel AJ, Massol F (Eds) Networks of invasion: A synthesis of concepts. Academic Press, London, 1–60. https://doi.org/10.1016/bs.aecr.2016.10.001

Davis MA (2003) Biotic globalization: Does competition from introduced species threaten biodiversity? Bioscience 53: 481–489. https://doi.org/10.1641/0006-3568(2003)053[0481:BGDCFI]2.0.CO;2

De Caceres M, Legendre P (2009) Associations between species and groups of sites: Indices and statistical inference. Ecology 90: 3566–3574. https://doi.org/10.1890/08-1823.1

Doherty TS, Glen AS, Nimmo DG, Ritchie EG, Dickman CR (2016) Invasive predators and global biodiversity loss. Proceedings of the National Academy of Sciences of the United States of America 113: 11261–11265. https://doi.org/10.1073/pnas.1602480113

Dormann CF, Gruber B, Frund J (2008) Introducing the bipartite package: Analysing ecological networks. R News 8: 8–11. http://CRAN.R-project.org/doc/Rnews/

Du Preez B, Purdon J, Trethowan P, Macdonald DW, Loveridge AJ (2017) Dietary niche differentiation facilitates coexistence of two large carnivores. Journal of Zoology 302: 149–156. https://doi.org/10.1111/jzo.12443

Duffy DC, Capece P (2012) Biology and impacts of Pacific island invasive species. The domestic cat (*Felis catus*). Pacific Science 66: 173–212. https://doi.org/10.2984/66.2.7

Fisher RN (1997) Dispersal and evolution of the pacific basin gekkonid Gekkonid lizards gehyra *Gehyra oceanica* and gehyra *Gehyra mutilata*. Evolution 51: 906–921. https://doi.org/10.1111/j.1558-5646.1997.tb03672.x

Gooch S, Ashbrook K, Taylor A, Székely T (2015) Using dietary analysis and habitat selection to inform conservation management of reintroduced Great bustards *Otis tarda* in an agricultural landscape. Bird Study 62: 289–302. https://doi.org/10.1080/00063657.2015.1050993

Gouni A, Sanford G (2003) L'avifaune de Niau (Polynésie française) en février 2003, cas particulier: Le Martin–Chasseur, *Todiramphus gambieri niauensis*. Société d'Ornithologie de Polynésie 'Manu', Papeete.

Gouni A, Kesler DC, Sarsfield R, Tehei T, Gouni J, Butaud J, Blanc L, Durieux J, Marie J, Lichtlé A (2006) Étude du Martin–chasseur des Gambier (*Todiramphus gambieri niauensis*) sur l'atoll de Niau. Société d'Ornithologie de Polynésie 'Manu', Papeete.

Hamilton AM, Zug GR, Austin CC (2010) Biogeographic anomaly or human introduction: A cryptogenic population of tree skink (Reptilia: Squamata) from the Cook Islands, Oceania.

Biological Journal of the Linnean Society 100: 318–328. https://doi.org/10.1111/j.1095-8312.2010.01437.x

Hebert PD, Stoeckle MY, Zemlak TS, Francis CM (2004) Identification of birds through DNA barcodes. PLoS biology 2(10): e312. https://doi.org/10.1371/journal.pbio.0020312

Holmes ND, Spatz DR, Oppel S, Tershy B, Croll DA, Keitt B, Genovesi P, Burfield IJ, Will DJ, Bond A, et al. (2019) Globally important islands where eradicating invasive mammals will benefit highly threatened vertebrates. PLoS ONE 14(3): e0212128. https://doi.org/10.1371/journal.pone.0212128

Holyoak DT, Thibault JC (1984) Contribution à l'étude des oiseaux de Polynésie orientale. Editions du Muséum, Paris.

Hsieh TC, Ma KH, Chao A (2016) iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7: 1451–1456. https://doi.org/10.1111/2041-210X.12613

Ineich I, Gouni A, Blanc L, Durieux J, Butaud J (2007) Lizards of Niau Atoll, Tuamotu Archipelago, French Polynesia. Herpetological Review 38: 491–492. https://www.academia.edu/22104651/Lizards_of_Niau_Atoll_Tuamotu_Archipelago_French_Polynesia

Jacobs J (1974) Quantitative measurement of food selection – A modification of the Forage Ratio and Ivlev's Electivity Index. Oecologia 417: 413–417. https://doi.org/10.1007/BF00384581

Kesler DC, Laws RJ, Cox AS, Gouni A, Stafford JD (2012) Survival and population persistence in the critically endangered Tuamotu kingfisher. Journal of Wildlife Management 76: 1001–1010. https://doi.org/10.1002/jwmg.324

Marie J (2006) Biodiversité, biologie de la conservation et recherches en entomologie médicale: Prospection entomologique sur l'atoll de Niau. Institut Louis Malardé, Papeete.

Marshall KN, Stier AC, Samhouri JF, Kelly RP, Ward EJ (2016) Conservation challenges of predator recovery. Conservation Letters 9: 70–78. https://doi.org/10.1111/conl.12186

McCreless EE, Huff DD, Croll DA, Tershy BR, Spatz DR, Holmes ND, Butchart SHM, Wilcox C (2016) Past and estimated future impact of invasive alien mammals on insular threatened vertebrate populations. Nature Communications 7: 1–11. https://doi.org/10.1038/ncomms12488

Mueller-Dombois DR, Forsberg F (1998) Vegetation of the tropical Pacific islands. Springer, New York. https://doi.org/10.1007/978-1-4419-8686-3

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2018) vegan: Community Ecology Package. https://CRAN.R-project.org/package=vegan

Parker ED, Selander RK, Hudson RO, Lester LJ (1977) Genetic diversity in colonizing parthenogenetic cockroaches. Evolution 31: 836–842. https://doi.org/10.1111/j.1558-5646.1977.tb01076.x

R Development Core Team (2018) R: A language and environment for statistical computing. http://www.R-project.org

Rankin EEW, Knowlton JL, Gruner DS, Flaspohler DJ, Giardina CP, Leopold DR, Buckardt A, Pitt WC, Fukami T (2018) Vertical foraging shifts in Hawaiian forest birds in response to invasive rat removal. PLoS One 13: e0202869. https://doi.org/10.1371/journal.pone.0202869

Reitz SR, Trumble JT (2002) Competitive displacement among insects and arachnids. Annual Review of Entomology 47: 435–465. https://doi.org/10.1146/annurev.ento.47.091201.145227

Resano-Mayor J, Real J, Moleón M, Sánchez-Zapata JA, Palma L, Hernández-Matías A (2016) Diet–demography relationships in a long-lived predator: From territories to populations. Oikos 125: 262–270. https://doi.org/10.1111/oik.02468

Schlaepfer MA, Sax DF, Olden JD (2011) The potential conservation value of non-native species. Conservation Biology 25: 428–437. https://doi.org/10.1111/j.1523-1739.2010.01646.x

Schlaepfer MA, Sax DF, Olden JD (2012) Toward a more balanced view of non-native species. Conservation Biology 26: 1156–1158. https://doi.org/10.1111/j.1523-1739.2012.01948.x

Seitre R, Seitre J (1992) Causes of land-bird extinctions in French Polynesia. Oryx 26: 215–222. https://doi.org/10.1017/S0030605300023747

Steadman DW (2006) Extinction and biogeography of tropical Pacific birds. University of Chicago Press, Chicago.

Tershy BR, Shen KW, Newton KM, Holmes ND, Croll DA (2015) The importance of islands for the protection of biological and linguistic diversity. Bioscience 65: 592–597. https://doi.org/10.1093/biosci/biv031

Thibault J, Cibois A (2017) Birds of Eastern Polynesia: A biogeographic atlas. Lynx, Barcelona.

Towns DR (2002) Korapuki island as a case study for restoration of insular ecosystems in New Zealand. Journal of Biogeography 29: 593–607. https://doi.org/10.1046/j.1365-2699.2002.00709.x

White EM, Wilson JC, Clarke AR (2006) Biotic indirect effects: A neglected concept in invasion biology. Diversity and Distribution 12: 443–455. https://doi.org/10.1111/j.1366-9516.2006.00265.x

White TE (1953) A method of calculating the dietary percentage of various food animals utilized by aboriginal peoples. American Antiquity 18: 396–398. https://doi.org/10.2307/277116

Wilmshurst JM, Hunt TL, Lipo CP, Anderson AJ (2011) High-precision radiocarbon dating shows recent and rapid initial human colonization of East Polynesia. Proceedings of the National Academy of Sciences of the United States of America 108: 1815–1820. https://doi.org/10.1073/pnas.1015876108

Zarzoso-Lacoste D, Corse E, Vidal E (2013) Improving PCR detection of prey in molecular diet studies: Importance of group-specific primer set selection and extraction protocol performances. Molecular Ecology Resources 13: 117–127. https://doi.org/10.1111/1755-0998.12029

Zarzoso-Lacoste D, Bonnaud E, Corse E, Gilles A, Meglecz E, Costedoat C, Gouni A, Vidal E (2016) Improving morphological diet studies with molecular ecology: An application for invasive mammal predation on island birds. Biological Conservation 193: 134–142. https://doi.org/10.1016/j.biocon.2015.11.018

Zavaleta ES, Hobbs RJ, Mooney HA (2001) Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology and Evolution 16: 454–459. https://doi.org/10.1016/S0169-5347(01)02194-2

Supplementary material 1

Estimates of prey relative availability and selectivity on Niau Island

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Data type: species data

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Link: https://doi.org/10.3897/neobiota.53.35086.suppl1

Supplementary material 2

Diet dataset obtained through morphological analyses

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Data type: measurement

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Link: https://doi.org/10.3897/neobiota.53.35086.suppl2

Supplementary material 3

Diet composition and breadth of the four studied predators

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Data type: measurement

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Supplementary material 4

Analysis of species richness and diversity

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Data type: statistical data

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